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Electrostatic forces in wind-pollination—Part 2: Simulations of pollen capture☆

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Abstract

During fair-weather conditions, a 100 V m^{-1} electric field exists between positive charge suspended in the air and negative charge distributed on the surfaces of plants and on the ground. The fields surrounding plants are highly complex reaching magnitudes up to 3×10^{6} V m^{-1}. These fields possibly influence the capture of charged wind-dispersed pollen grains. In this article, we model the electric fields around grounded conductive spherical "plants" and then estimate the forces and resulting trajectories of charged pollen grains approaching the plants. Pollen grain capture depends on many factors: the size, density, and charge of the pollen; the size and location of the plant reproductive structures; as well as wind speed, ambient electric field magnitude, and air viscosity. Electrostatic forces become increasingly important as pollen grain charge increases and pollen grain size (mass) decreases. A positively charged pollen grain is attracted to plants, while a negatively charged pollen grain is repelled. The model suggests that a pollen grain (10 μm radius, carrying a positive charge of 1 fC) is captured if passing within 2 mm of the plant. A similar negatively charged pollen grain is repelled and frequently uncapturable. The importance of electrostatic forces in pollen capture is limited by wind, becoming virtually irrelevant at high wind speeds (e.g. 10 m s^{-1}). However, during light wind conditions (e.g. 1 m s^{-1}), atmospheric electricity may be a significant factor in the capture of wind-dispersed pollen.

Keywords: Atmospheric electricity; Electrostatic charge; Electrostatic field; Particle capture; Wind pollination

1. Introduction

The transfer of pollen grains between plants is integral to reproduction for wind-pollinated plants. Following release, the pollen grains are carried by the wind, with most depositing on nearby plants and the ground shortly after release. Successful capture is limited, in part, because the female pollen-capturing structures, called stigmas, present tiny targets (e.g. a few millimeters long) for the minute (e.g. 10 μm radius) pollen grains. Furthermore, the pollen grains tend to follow the wind as it flows around the flowers, passing by the receptive stigmas and avoiding capture (Rubenstein and Koehl, 1977; Shimeta and Jumars, 1991). Adaptations in plant

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morphology that enhance pollen capture should be favored by natural selection.

Electric fields are present in the environment, and wind-dispersed pollen grains are electrically charged (Bowker and Crenshaw, 2006). Consequently, as charged airborne pollen grains encounter the electric fields in the environment around plants they may experience an electrostatic force sufficient to influence deposition. Electrostatic enhancement of capture has been demonstrated in agricultural settings, where purposeful electrostatic charging of pesticides or pollen increased deposition by up to an order of magnitude (Felici, 1973; Law, 1987, 2001; Gan-Mor et al., 1995; Gan-Mor et al., 2003; Banerjee and Law, 1996; Law et al., 1996; Law et al., 2000; Bechar et al., 1999; Vaknin et al., 2000, 2001; Law and Scherm, 2005).

This is the second in a series of two articles exploring the role of electrostatic forces in pollen grain capture under natural conditions. The electrostatic force on a charged wind-dispersed pollen grain is the product of two factors; the electric field at the pollen grain's location and its charge. In the companion article (Bowker and Crenshaw, 2006), we report measurements of the electrostatic charge carried by pollen grains. In this article, we develop a simple model of the natural electrostatic field around plants based on plant size (morphology), location, and the magnitude of the ambient electric field. Then, we use the pollen grain charge measurements (Bowker and Crenshaw, 2006) and the model of the electric field around plants to estimate the electrostatic force on pollen grains and simulate their trajectories as they pass near plants.

During "fair-weather" conditions, characterized by clear skies and light breezes, the atmosphere has a slight preponderance of positive ions, giving the air a small net positive charge (a positive space charge). The space charge is between 10^4 and $10^6\,\mathrm{m}^{-3}$ (Chalmers, 1967). Collectively, the surface of the earth and the plants and animals in electrical contact with it, carry a net negative charge equal to the cumulative atmospheric positive space charge (Fig. 1), even though the ground is defined to have an electrical potential of zero volts. This charge separation generates the "fair-weather" electric field averaging nearly $100\,\mathrm{V\,m}^{-1}$ at the surface of the earth. Globally, a diurnal variation of approximately 20% in the field is present, but this can often be obscured by local effects (Chalmers, 1967). Variation in weather, air conductivity, or the presence of pollution, space charge, or topography

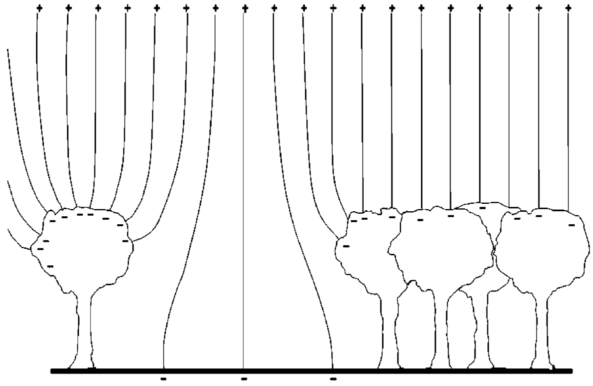

Fig. 1. Electric field lines around a solitary tree, above a forest, and above a grassy field. The lines are tangent to the electric field. The strength of the field is inversely proportional to the spacing of the lines. The lines extend from atmospheric positive charge to negative charge on the ground and on the surfaces of trees. The negative charge is most concentrated on the solitary tree and on the edge of the forest and is nonexistent beneath the solitary tree and within the forest. In the grassy field, between the solitary tree and the forest, the electric field is reduced.

can lead to orders of magnitude changes as well as polarity reversals in the local electric field.

The negative charge on plants is asymmetrically distributed, with charge concentrated on pointed plant features (e.g. tips of branches, edges of leaves, and feathery plant stigmas) that extend above their surroundings. Though not well described, the local electric field around these features derived from the distribution of negative charge is complex and magnified (Maw, 1961a, b, 1963; Corbet et al., 1982; Erickson and Buchmann, 1983; Niklas, 1985; Bechar et al., 1999; Vaknin et al., 2001). The magnification of electric fields around plants is described for electrostatic applications in agriculture, where the electric field forms between a charged spray cloud (of pollen grains or pesticide) and the plant. The electric field around the points of the plant can reach values of several hundred thousand volts per meter (Law, 1987, 2001; Dai and Law, 1995; Bechar et al., 1999). Consequently, the charged spray is often deposited on the points of the plant, as well as on surfaces that generally do not capture particles—such as the underside of a leaf (Erickson and Buchmann, 1983; Law, 1987, 2001; Dai and Law, 1995; Law and Scherm, 2005). Through a similar magnification process, we expect the natural electric field around plants can be many orders of magnitude (e.g. $>100\,\mathrm{kV\,m}^{-1}$) larger than the ambient field (e.g. $100\,\mathrm{V\,m}^{-1}$). A simple model of the electric fields surrounding plants is developed in this article.

The role of electrostatic forces in pollen grain capture depends on pollen attributes. Wind-dispersed pollen grains are small (10–20 μm radius), dry, and generally smooth and have gravitational settling velocities between 0.02 and $0.06\,\mathrm{m\,s^{-1}}$ (Whitehead, 1983). At release, they often carry relatively large (on average, ~0.8 fC in magnitude) quantities of electrostatic charge, although some carry charges up to 40 fC in magnitude (Bowker and Crenshaw, 2003, 2006). The pollen charge distributions are bipolar, with some pollen grains positively charged and others negatively charged (Bowker and Crenshaw, 2006). During fair-weather conditions, positively charged pollen grains would be strongly attracted to plants while negatively charged pollen grains would be repelled. It is likely that most pollen grains retain a substantial portion of their initial charge throughout dispersal since the electrostatic neutralization time, or the time required for a pollen grain to lose its charge (time constant 440 s), is long relative to its dispersal time (seconds to minutes) (Bowker and Crenshaw, 2003, 2006).

The object of this paper is twofold: (1) to explore the nature of the electric fields surrounding plants, deriving their magnitudes and directions as a function of plant morphology and the ambient electric environment; and (2) to use a simple mathematical model to calculate the forces and trajectories of charged pollen grains as they approach a plant and encounter its surrounding electric field to determine how factors such as pollen grain charge and size, plant size, and prevailing wind speed influence pollen capture.

2. Materials and methods

2.1. Derivation of electric fields around plants in nature

During fair weather conditions, negative charge is induced on the ground and on the surface of plants. Because plants are conductive (resistance ~20 kΩ from stigma tip to floral pedicil, Corbet et al., 1982), charge can move through them, ultimately migrating to surfaces at high, exposed, skyward facing locations. The charge on the plant is distributed (in an asymmetrical manner, determined by plant geometry) such that every location has the same potential (in this case ground potential, or 0 V). The resulting electric field is perpendicular to the plant's surface and is directly proportional to the magnitude of the surface charge.

Determining surface charge distributions and the electric fields surrounding plants requires information about their complex shapes and charges. For simple shapes, e.g. spheres, flat plates, cylinders, analytical solutions for the surrounding electric fields can be found. For more complex shapes, solutions for the electric field are most easily obtained using finite element models (e.g. Quickfield 3.4–Tera Analysis Ltd.).

The simple case of an isolated, charged (magnitude Q), conductive sphere (radius, A) illustrates how shape affects the surrounding electric field. The electric field ($\mathbf{E}_\mathrm{s}$) outside the sphere ($r>A$) is inversely proportional to the square of the distance from the center of the sphere (r)

$$E_\mathrm{s} = \frac{Q}{4\pi\,\varepsilon_0 r^2}\hat{r} = \frac{\Phi_\mathrm{s}}{r}\hat{r}, \tag{1}$$

where Φ_s is the electric potential of the sphere relative to the potential at infinity, and $\hat{r}$ is a unit vector in the radial direction. The largest electric fields are found when r is small, maximally at the surface when r equals A. For spheres with constant Q and various radii (A), small decreases in A lead to drastic increases in the surface electric field. This relationship is consistent for objects with complex geometries. Thus, purely as a consequence of their shape, the electric fields around small or sharp objects (e.g. stigmas, leaf edges, and tree tops) can easily be orders of magnitude greater than around larger or smoother objects.

However, charge is not constant, but varies with plant size, height above its surroundings, and the magnitude of the ambient electric field. To approximate the charge, we model the grounded plant as an isolated, charged, conductive sphere with a potential of 0 V a height (h) above the ground in a uniform vertical electric field (E_0). At the height of the sphere, the air has a potential equal to the product of the height and the ambient electric field (e.g. 100 V for a plant one meter above the ground in a $100\,\mathrm{V\,m^{-1}}$ electric field). Thus, a potential difference exists between the sphere and the surrounding air. If the sphere was not electrically connected to ground, it would be at equipotential with the surrounding air, essentially being uncharged. However, to maintain its potential at ground (0 V) it carries a negative charge

$$hE_0 = \frac{Q}{4\pi\,\varepsilon_0 A}. \tag{2}$$

The electric field ($\boldsymbol{E}_{\text{sur}}$) around a grounded sphere in the earth's electric field can be approximated by inserting the charge of the sphere (rearranging Eq.(2), noting that the charge is negative) into the equation for the electric field around a sphere (Eq. (1))

$$E_{\text{sur}} = \frac{-AE_0h}{r^2}\hat{r}, \tag{3}$$

where $\hat{r}$ is a unit vector pointing in a radial direction with its origin at the center of the sphere.

2.2. Model of pollen capture

The model of pollen capture, created in Matlab 6.1, attempts to predict the motion and capture of the pollen based on the electrostatic force, the image force, the gravitational force, and the wind force acting on the pollen during fair weather electric conditions. The goal was to determine the distance from the plant that the pollen grains can be captured and to see how this distance changes as the forces are varied.

For simplicity, some assumptions are made: First, the plants are perfectly conductive, electrically grounded, and spherical (radius A, 0.01, 0.001, and 0.0001 m). Secondly, the plant's surrounding electric field is given by Eq. (3), with the plants centered 1 m above the ground in an ambient electric field E_0 of 100 V m^{-1}. The electrostatic force ($\mathbf{F}_{\text{E}}$) on the pollen is the product of the electric field at the pollen's location ($\boldsymbol{E}_{\text{sur}}$, Eq. (3)) and the pollen's charge (q)

$$F_{\text{E}} = E_{\text{sur}}q. \tag{4}$$

A charged pollen grain of either polarity approaching the plant induces an opposite charge on the surface of the plant and is attracted. This "image" force depends on the distance of the pollen from the surface and is important when it is within a millimeter of the plant surface (Law, 1987, 2001). For a sphere, the image force ($\boldsymbol{F}_{\text{i}}$) on the pollen (for $r > A$) is

$$F_{\text{i}} = \frac{-Aq^2}{r4\pi\,\varepsilon_0(r-(A^2/r))^2}\hat{r}, \tag{5}$$

where r is the distance from the center of the sphere to the location of the pollen grain.

The pollen grains move under the action of these forces depending on their physical characteristics, such as size, shape, and mass. The pollen grains are modeled as spheres (with varying radii of 5, 10, and 20 μm), with a density equal to that of water (Paw and Hotton, 1989). Electrostatically, they are modeled as point charges (10, 1, 0.1, −0.1, −1, and −10 fC) where 1 fC is 6250 elementary charges. This range reflects the majority of pollen charges measured by Bowker and Crenshaw (2003, 2006). The gravitational force ($\boldsymbol{F}_{\text{g}}$) on the pollen equals the product of its mass (M, the product of its density, ρ, and volume) and the gravitational constant, $\mathbf{g}$ (9.8 m s^{-2})

$$F_{\text{g}} = Mg = \tfrac{4}{3}\pi\,\rho a^3 g, \tag{6}$$

where a is the radius of the pollen.

The trajectory of a pollen grain can be extrapolated from the wind velocity and the forces acting on the pollen. Each force accelerates the pollen until it reaches "terminal velocity" where the net force is exactly balanced by drag. The pollen is assumed to instantaneously reach terminal velocity. Furthermore, the pollen moves at low Reynolds number (i.e. Stokes drag applies). Consequently, the terminal velocity of the pollen, $\mathbf{U}$, is linearly dependent on the net force (Vogel, 1994)

$$F_{\text{D}} = 6\pi\mu Ua, \tag{7}$$

where the net force acting on the pollen is exactly equal to the force of drag $\boldsymbol{F}_{\text{D}}$ on the pollen and μ is the dynamic viscosity of air (1.8×10^{-5} kg m^{-1} s^{-1}).

The pollen grain initially starts 0.1 m above (gravity present, no wind forces) or 0.1 m to the side (gravity absent, wind forces present) of the spherical capture plant, itself positioned with its center at the origin (Fig. 2). The velocity of the pollen is calculated and then the pollen moves one step, less than one micrometer. This process is repeated until the pollen is either captured by the plant, or passes by uncaptured. The starting location of the pollen is moved horizontally to the side in progressively smaller increments until the pollen is no longer captured (and the moving increment is less than 10 μm). The capture distance is measured as the maximum difference in starting locations between an uncharged pollen grain (that moves in a straight line and is captured at the edge of the plant) and a charged pollen grain that is almost not captured (Fig. 2).

The wind is modeled as a constant horizontal velocity of 0, 1, or 10 m s^{-1}. No attempt in this model is made to account for the variation in wind velocity as the air diverges around the plant, for the turbulent airflow patterns behind the plant, or for the differences in wind velocity near the plant's surface (the velocity gradient).

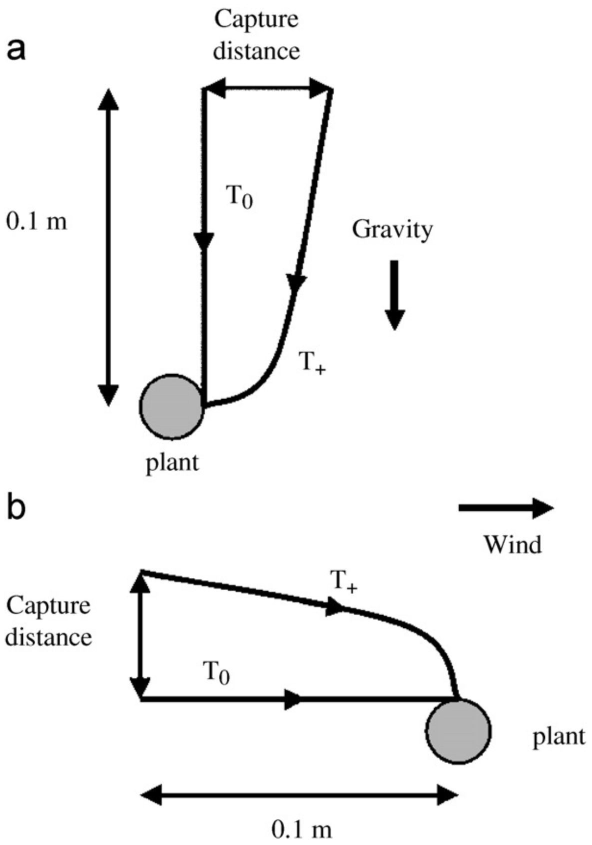

Fig. 2. Trajectories of uncharged (T_0) and positively charged (T_+) pollen grains as they approach a negatively charged spherical plant (gray). (a) An elevation-view showing trajectories experiencing the electrostatic force and gravity and (b) a plan-view showing trajectories experiencing the electrostatic force and wind. Capture distance is the difference in the starting locations between the uncharged and charged pollen.

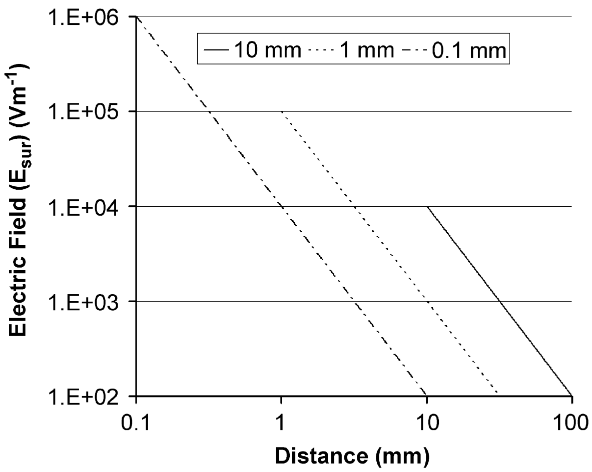

Fig. 3. The magnitude of the electric field (Eq. (3)) as a function of the distance from the center of three spherical "plants" (radii, 10, 1, 0.1 mm). The plants are 1 m above their surroundings in a $100\,\mathrm{V\,m^{-1}}$ ambient electric field. The origin of each line (upper left point of each line) shows the electric field at the surface of the sphere.

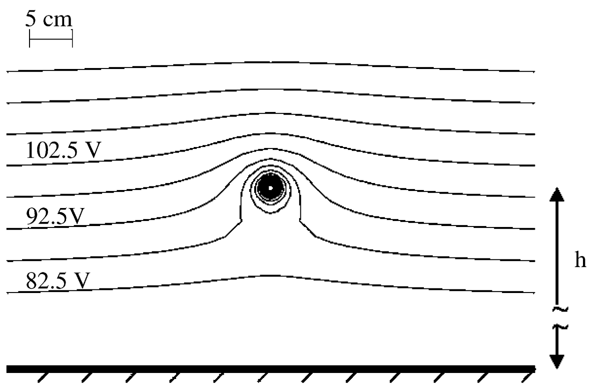

Fig. 4. Elevation view showing equipotential lines around a negatively charged a sphere (radius 0.01 m), 1 m above the ground, in a $100\,\mathrm{V\,m^{-1}}$ electric field. Equipotential lines (5 V increments) are concentrated locally around the sphere indicating a large surrounding electric field.

3. Results

Based on Eq. (3), the magnitude and the extent of the local field around a plant depend on its size, shape, and height above surroundings, with the strongest fields near the surfaces of sharp features (e.g. a branch, a blade of grass, a stigma). For example, a grass with a grounded spherical inflorescence, or panicle, of radius 0.01 m that is 1 m above its surroundings in an ambient field of $100\,\mathrm{V\,m^{-1}}$ has a surface electric field of $10\,\mathrm{kV\,m^{-1}}$ (Fig. 3). The equipotential lines around this plant are distorted (Fig. 4) and no longer parallel and horizontal as they would be for an uncharged sphere. For a tree (10 m tall, radius 5 m), such as the leftmost "tree" in Fig. 1, the electric field at the edge of the canopy is merely $200\,\mathrm{V\,m^{-1}}$. However, further magnification of the field would be found along the edge of each outermost leaf and at the tip of each branch.

As charged wind-dispersed pollen grains approach a plant, they experience significant electrostatic forces and their trajectories are altered. Electrostatic forces are most important when winds are light (near $0\,\mathrm{m\,s^{-1}}$). Pollen (10 μm radius) can be attracted from millimeters (pollen charge 1 fC) or even centimeters (10 fC) away from plants. Pollen (1 fC) can be captured up to an order of magnitude farther away compared with the radius of the plant part (e.g. 0.9 mm from a 0.1 mm plant radius, compared with just 2 mm from a 0.1 m plant radius). The largest plants capture pollen from the greatest distance (Fig. 5a). Relative to their size, the smallest plants are more effective at filtering pollen from the surrounding air, capturing pollen (10 fC, 10 μm radius) up to 31 plant radii away (Fig. 5b). Even modestly charged negative pollen grains (−0.1 fC) are uncapturable around the sharpest points (0.1 mm), while moderately charged negative pollen grains (−1 fC) are capturable only by the largest plants (0.01 m).

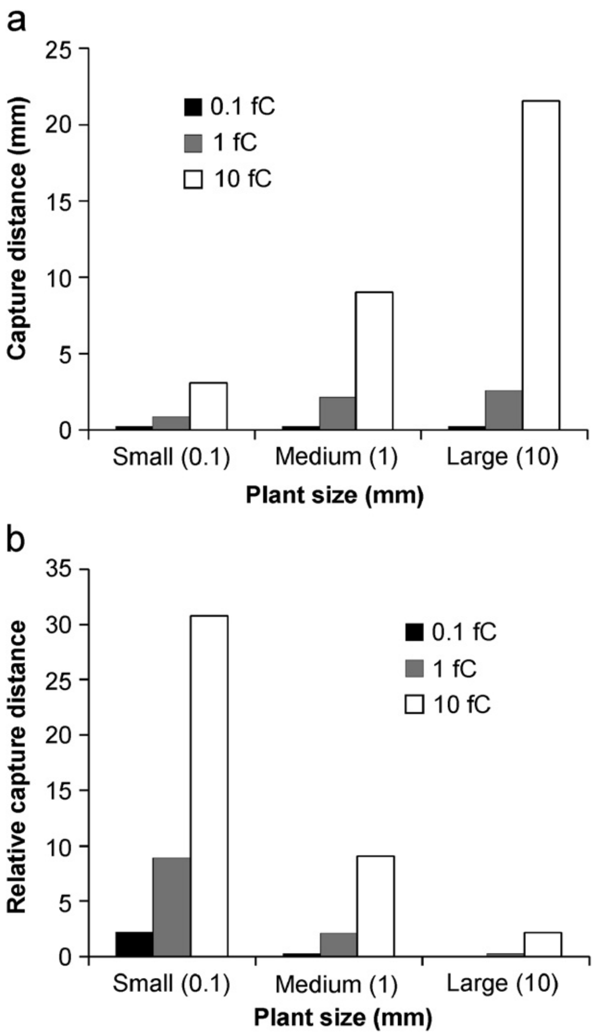

Fig. 5. (a) Capture distance (m) and (b) Relative capture distance (capture distance divided by plant radius) as a function of plant size, for pollen 10 μm in radius with one of three common positive charges.

Pollen size influences pollen capture, with the smallest pollen (5 μm radius) being most affected by electrostatic forces. For large pollen (20 μm radius) electrostatic forces influence capture only for highly charged pollen in the large electric fields around the smallest plants.

In the presence of wind (1, 10 m s^{-1}), electrostatic forces decrease dramatically in importance. Positively charged pollen is only electrostatically attracted from micrometers or tens of micrometers from the plant rather than the millimeters or centimeters in negligible wind. Furthermore, the wind becomes so strong that the repulsive force between the plant and the negatively charged pollen grains is not sufficient to prevent capture by impaction.

4. Discussion

Even though the ambient electric field is just 100 V m^{-1} during fair weather conditions, it is magnified (sometimes $>10^5$ V m^{-1}) around plants. The magnitude of the field is directly proportional to the height of the plant feature above its surroundings and inversely proportional to the square of its size (Eq. (3)). The fields are strongest, but drop off most rapidly, around fine points (e.g. stigmas, leaf edges). The fields may influence pollen capture as well as the deposition of ions, large charged wind-dispersed particles (dust, pollution particles), and charged radioactive products.

The magnification of ambient fields around stigmas by floral morphology has been shown to increase deposition of purposefully charged wind-dispersed pollen grains (Bechar et al., 1999; Vaknin et al., 2001). In the companion article (Bowker and Crenshaw, 2006), we have shown that, at release, wind-dispersed pollen grains are naturally charged. Most carry about 0.8 fC of charge in magnitude, but some carry charges up to 40 fC in magnitude. The pollen grain charge distributions for many plant species are bipolar, with some pollen grains carrying positive charges and others carrying negative charges (Bowker and Crenshaw, 2006). Generally, charged pollen grains (0.1–1 fC) experience substantial forces in fields greater than 10 kV m^{-1}, with larger fields (e.g. >100 kV m^{-1}) usually necessary for electrostatic forces to equal gravity (Bowker and Crenshaw, 2006).

The simulations of pollen grain trajectory presented here suggest that electrostatic forces influence the motion of even weakly charged pollen grains. Pollen grain size (e.g. mass) influences capture, with electrostatic forces most important for small (light) pollen and inconsequential for large (heavy) pollen (e.g. corn, *Zea mays*, radius 50 μm).

Positively charged pollen grains passing within a millimeter or two from the negatively charged surface of the plant are captured. The large plants (10 mm radius) capture pollen over the greatest distances, up to 74 mm away for the smallest most highly charged pollen (5 μm radius and 10 fC). However, relative to their size, small plants (0.1 mm), with their large magnitude but localized electric fields, are most efficient at capturing pollen, even up to 31 plant radii away.

Negatively charged pollen grains are repelled by the negatively charged plants, with small plants repelling virtually all negatively charged grains. Pollen grains with weak (0.1 fC) negative charges are still captured by the largest plants, although some pollen is repelled and lost that would otherwise settle on the plant in the absence of electrostatic forces. Furthermore, negatively charged pollen that is captured is not likely to deposit on points (e.g. the stigma) where the fields repelling them are largest. This indicates that an entire class of pollen may have difficulty fertilizing plants, possibly suggesting the reason why pollen charge distributions for several plant species (*Juniperus virginiana* and *Pinus taeda*) are biased in the positive direction (Bowker and Crenshaw, 2006).

The importance of electrostatic forces diminishes in the presence of wind forces, decreasing the capture distances for positively charged pollen grains, but permitting the capture of negatively charged pollen grains. The wind limits the time the pollen spends in the high field regions around the plant and thereby limits the ability of electrostatic forces to influence the motion of the pollen. Basically, electrostatic forces are only larger than wind forces in extreme circumstances (extremely small, highly charged pollen encountering a small plant). However, these simulations do not account for the complex airflow patterns and gradients in wind velocity around the plant, where the wind speed is much lower. Pollen grains in these regions will move more slowly and electrostatic forces will likely influence their capture.

As a charged pollen grain approaches the plant, it induces a charge of opposite polarity, an image charge, on the surface. The image force is always attractive and gets extremely large as the charged pollen approaches the plant's surface. In concurrence with Law (1987, 2001), these simulations suggest the image force only modestly increases capture distance (2% maximum, or a few millimeters, for 10 μm pollen), however, it is crucial in the final stages of capture and, in nature, may even help the pollen stick after capture (Chaloner, 1986). Once it passes within several micrometers, a charged pollen grain (of either polarity) will inevitably be captured. Since the image force is always attractive, during pollen release the pollen must be flung far enough away from the plant to avoid immediate recapture.

During typical pollination conditions (fair-weather and light breezes), it is likely that electrostatic forces are important in pollination, increasing the number and the efficiency of pollen grain capture. Consequently, there may be ecological and evolutionary implications of electrostatic forces on pollen and flower morphology and on dispersal strategies. However, since they would most likely select for similar morphologies (e.g. feathery stigmas), it is difficult to disentangle the influence of electrostatic forces from aerodynamic forces. Direct measurements of electrostatic pollen capture in nature, as well as refined model descriptions of the airflow and electric field patterns around morphologically-correct plants could be used to further explore the role of electrostatic forces in wind pollination.

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